

TWO NEW SEMI-AQUATIC SPECIES OF *DIPLOTREMA* (OLIGOCHAETA: MEGASCOLECIDAE: ACANTHODRILINAE), WITH A RE-DESCRIPTION OF THE TYPE SPECIES

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Dyne, G.R. & Jamieson, B.G.M. 1998 06 29: Two new semi-aquatic species of *Diplo-trema* (Oligochaeta: Megascolecidae: Acanthodrilinae), with a re-description of the type species. *Memoirs of the Queensland Museum* 42(2): 487-493. Brisbane. ISSN 0079-8835.

Two new species of the genus *Diplo-trema* sharing a suite of morphological characters and a semi-aquatic mode of life are described. Together with the previously described *D. tyagarah*, they are placed in a species-group the nominate species of which is the generic type-species, *D. fragilis*. The latter taxon, of pivotal importance in early phylogenetic schemes owing to an erroneous determination of the condition of the male pores, is redescribed from the syntypes. □ *Earthworms, Megascolecidae, Diplo-trema, semi-aquatic.*

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The significance of the type-species of *Diplo-trema*, *D. fragilis* Spencer, in the inferred phylogeny of the Megascolecidae proposed by Stephenson (1930) has been outlined by Jamieson (1971) and Dyne (1978). More recent studies (Jamieson & Dyne, 1976; Dyne, 1984) have shown that the genus is far more widespread and speciose than previously believed, and that distinct species-groups are recognisable.

The two new species described here confirm the concept of a species-group including the type-species of the genus and a number of morphologically similar species inhabiting a similar ecotype. The collection of these species at sites either subject to periodic inundation, or permanently below the water-table, testifies to their semi-aquatic propensities. This represents exploitation of a niche largely unfilled by other Australian megascolecids. Some *Spenceriella* species are known from swampy habitats, however (Dyne, 1984).

SYSTEMATICS

Members of the *Diplo-trema fragilis* species-group share the following character set: prostomium epilobous, nephropores in the vicinity of *cd*, slender body form, ♂ pores slightly presetal, intersegmental markings restricted to the region of segments XVI-XX, genital seta follicles strongly developed in VII, VIII or IX, often with associated glands, penial setae fine and delicate with little or no ornamentation, pharyngeal tufted nephridia absent, large glandular mass (here termed 'ventral glands') located under the nerve-cord in XVII-XIX, spermathecae divided into a subspherical ampulla and short, blunt digitiform

diverticulum bearing numerous sperm chambers on its inner surface (*D. helonoma* diverges somewhat from this latter state).

It should be noted, however, that most of these unifying characteristics are symplesiomorphies: only the possession of pharyngeal tufting, genital seta glands and ventral glands represent probable synapomorphies.

Five new species of *Diplo-trema* from south and central Queensland were recently partly described and sketched (Blakemore, 1997). Four of these differ from the *fragilis* group in lacking anterior nephridial tufting. A fifth, *D. ambrosensis*, has anterior tufts, but, as for the other species, the form and sculpturing of the penial, and genital, setae is not described, considerably impeding comparison, and no reference is made to ventral glands. As the penisetal follicles are described as 'enormous', it is unlikely that *D. ambrosensis* belongs to the *fragilis* group.

KEY TO SPECIES OF THE *DIPLOTREMA FRAGILIS* SPECIES-GROUP

1. Dorsal pores present . . . . . 2  
Dorsal pores absent . . . . .  
. . . . . *D. proserpinensis* sp. nov.
2. Prostatic glands long, extending at least into segment XXI . . . . . *D. fragilis* Spencer  
Prostatic glands not extending beyond XX . . . . . 3
3. Gizzard rudimentary; first dorsal pores in the vicinity of 19/20; conspicuous glands associated with the genital setae. . . . *D. helonoma* sp. nov.  
Gizzard well-developed; first dorsal pores in the vicinity of 7/8; no conspicuous glands associated with the genital setae. . . . *D. tyagarah* Dyne

***Diploptrema fragilis* Spencer, 1900**  
(Fig. 1)

*Diploptrema fragilis* Spencer, 1900: 31-32 pl. 4, figs 4-6.

*Diploptrema fragilis*: Sweet, 1900: 114-5 pl. 14, fig. 6.

*Diploptrema fragilis*: Michaelsen, 1907: 142.

*Plutellus (Diploptrema) fragilis*: Michaelsen, 1916: 61.

*Diploptrema fragilis*: Jamieson, 1971: 100-102.

**MATERIAL.** Many specimens examined, 1 closely (condition poor). **SYNTYPES:** National Museum of Victoria G31. Approx. 25°37'S, 151°37'E., Gayndah, Sept., 1891-Qld.

**DESCRIPTION.** Length = 31mm. Width = 2.0mm. Segments = 111. Form cylindrical, anterior end blunt and rounded, slightly bulbous, pigmentless buff in alcohol. Prostomium closed, epilobous 1/2; first dorsal pore (perforate) in 9/10. Setae 8 per segment, closely paired, the ventral setal couples of XVIII present, those of XVII and XIX modified as enlarged penial setae, those of VIII and IX as genital setae. Nephropores not visible.

Clitellum annular, weaker ventrally, over XIII-XVI, dorsal pores obscured, intersegmental furrows and setae only sporadically visible. ♂ pores minute orifices equatorial, in XVIII. ♂ field an approximately circular, somewhat tumid area extending longitudinally from the setal arc of XVI to that of XIX, and laterally, in XVIII, beyond *b*-lines, small, indistinct, transversely oval papillae (the prostatic porophores) present in XVII and XIX, at the sites of the modified ventral setal couples. ♀ pores minute orifices in a pair of considerable papillae in front of *a* setae, on XIV. Spermathecal pores on a pair of elliptical, slender papillae, in 7/8, 8/9, with centres in *b*.

Accessory markings: a pair of horny ridges posteriorly in XIV, median to *a* (evidently misidentified by Spencer as the ♀ pores); a median transversely elliptical prominence in 17/18 is possibly a normal feature of the species. Segment VIII glandular, and appreciably widened.

Septa: 5/6 slightly, 6/7 and 7/8 moderately strongly, and 8/9 and 9/10 very strongly thickened, the succeeding three septa slightly thickened, remainder thin. Pharyngeal glands well-developed, forming several tiers of flattened, shortly palmate lobes in III, anteriorly. Dorsal blood vessel single, continuous to the posterior portion of the pharynx, flattened and adherent to the intestine in XIV posteriorly; last hearts in XIII, those of X-XIII large, and increasing slightly in size posteriorly, supra-oesophageal vessel present, but its limits not determinable because of maceration. Gizzard large, glossy, but thin-walled, in V. Oesophagus narrow, VI-XIV,

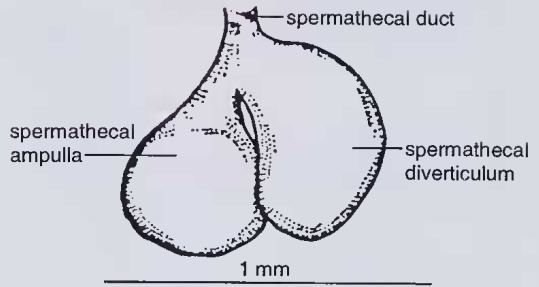


FIG. 1. *Diploptrema fragilis* Spencer, 1900. Right spermatheca of segment IX. Syntype (NMVG31).

calciferous glands or other elaborations absent; intestine commences with abrupt expansion in XV, reaching full width in XVI, a definite typhlosole lacking.

Nephridia exclusively holonephric, commencing in II, each invested in a high peritoneum and forming a regular, simple lobe on each side, in each segment; ducts long and avesciculate, entering the parietes in *c*-lines. Pharyngeal tufting absent.

Holandric: large, thick-walled spermatic funnels present in X and XI; seminal vesicles 2 pairs of compact, lobulated, and fairly small masses in XI and XII. Prostatic glands 2 pairs of flattened, tubular organs, the anterior pair extending to XXII, the posterior set to XXIII. The glands are sinuous, with each bend contiguous with the next, ducts abruptly demarcated, slender, glossy, and running almost straight medianly. Anterior prostates approximately twice the size of the posterior pair, though the length of the ducts is similar; the ducts enter a median, internal glandular mass extending from XVII to XIX, and corresponding with the external manifestation of the ♂ field. Two penial seta follicles enter the glandular mass in the vicinity of the prostatic ducts, each with several setae; the setae slender, narrowly pointed, basally often expanded, gently curved or slightly sinuous, with the ectal 1/4 curved through as much as a right angle, the ectal end simple, or with a crumpled appearance; minute notching present on the shaft, mostly almost inappreciable. Length mature seta = 1.4mm (mean of 2), midshaft diameter = 40µm. Ovaries moderately stout, long, linguiform lobes of several large, irregularly arranged oocytes; funnels moderate-sized, simple, also in XIII. Spermathecae 2 subequal pairs, in VIII and IX, each with a medianly directed ovoid, or spherical ampulla and a lateral, equisized or somewhat longer, iridescent concavo-convex

diverticulum. The ampulla and diverticulum share a short narrow duct; length right spermatheca of 1X (base of ampulla to pore) = 0.64mm. A battery of genital setae present in segments VIII and IX, located behind each spermathecal duct; the setae gently curving, with a broad point, ornamented with the deep, elongate, crescentic notching characteristic of such setae in acanthodrilids, from very near the tip to slightly less than halfway down the shaft, length mature seta = 9.98mm, midshaft diameter = 40 $\mu$ m (mean of 2).

REMARKS. There can be no doubt that the re-examined specimen is conspecific with the material described by Spencer (1900) as *Diplo trema fragilis*, the type of a new genus. The specimen presumably contributed to the description. Points of agreement in Spencer's account which confirm the identity of the re-examined specimen are: the epilobous prostomium, the large oval midventral glandular patch in XVI-XIX, and the swollen, glandular appearance of segment VIII. With respect to the position of the  $\delta$  and prostatic pores, however, Spencer's account is erroneous, a departure from his usual accuracy, possibly because of the small size of the species. No credence can now be placed on his observation of only a single pair of prostates with pores behind the  $\delta$  pores on XVIII; the re-examined specimen has two pairs of prostatic pores, on XVII and XIX, with the  $\delta$  pores quite separate, on XVIII, as demonstrated by Jamieson (1971). The presence of an additional pair of prostatic glands was first noted by Sweet (1900) in her re-examination of *D. fragilis*, though she termed these prostates 'accessory glands'. All of the type-specimens, despite their poor condition which precludes illustration of the genital field, are clearly referable to a single species.

Accepting Spencer's original description, Michaelsen (1910) placed *D. fragilis* within a monotypic section of the Acanthodrilinae, the Diplo tremacea. A subsequent examination of New Caledonian species (Michaelsen, 1913) genuinely having the  $\delta$  and prostatic ducts separate on XVIII (as erroneously described by Spencer, 1900, for *Diplo trema fragilis*), convinced Michaelsen that such an arrangement was closer to the plutelloid (and hence, Megascolecina) grade of organisation than to the acanthodrilin system. Accordingly, the latter species and *D. fragilis* were referred to a separate subgenus within *Plutellus*. The seemingly transitional condition of the  $\delta$  terminalia in this group resulted

in the incorporation of *Plutellus* (*Diplo trema*) into a phylogenetic scheme (Michaelsen, 1916, 1921), endorsed and expanded by Stephenson (1930) where it occupied an intermediate position, separating '*Acanthodrilus*' from the truly megascolecina *Plutellus*. Stephenson adopted the term 'accessory prostates' for the organs illustrated by Sweet, while continuing to accept Spencer's original diagnosis for the genus.

After the true status of *D. fragilis* became known, the New Caledonian forms remained within the *Plutellus* congeries until accommodated within the newly erected genus *Eudiplo trema*. The uniqueness of the  $\delta$  system in these species has thus been satisfactorily recognised (Jamieson & Bennett, 1979). The authors have attempted unsuccessfully to collect fresh material of *D. fragilis*, although a further quite distinct undescribed *Diplo trema* species was recovered by GD from the banks of the Burnett River at Gayndah, southeastern Queensland (SEQ).

#### *Diplo trema helonoma* sp. nov. (Figs 2, 3)

ETYMOLOGY. Latin, *helonoma*, a dweller in the marshes.

MATERIAL. (Holotype and 4 paratypes examined in detail) HOLOTYPE: ANICGD.95.144.1. BanBan Springs (25°41'S, 151°49'E), SEQ, in black swampy soil at and below the water table. Coll. G. Dyne and A. Postle, 9 June 1974: Numerous clitellates, immature specimens and fragments; PARATYPES: ANICGD.95.144.1, collection data as for holotype. FURTHER MATERIAL: ANICGD.95.144.1. Same locality, at side of spring, Coll. B. Jamieson and E. Bradbury, 21 May 1971: Numerous specimens (mostly acitellate), not designated as type material.

DESCRIPTION. Length > 24mm, 113mm. Width (midclitellar) = 2.8mm. Segments ?, 182 (H - posterior amputee, P1). Pigmentless buff in alcohol, clitellum with a pinkish tinge, particularly in freshly preserved material. Prostomium epilobous 1/3, closed. First dorsal pore 19/20 (H, P1), dorsal pores generally indistinct. Setae regularly disposed in 8 rows, uniform in size with the exception of the ventral setae of XVII and XIX, which are enlarged as penial setae, and those of VIII and IX, modified as genital setae; ventral setal couples of XVIII present. Nephropores visible as minute depressions immediately anterior to *c* in each segment, by a distance slightly exceeding *cd*.

Clitellum annular, obscuring the intersegmental furrows, though the setae remain prominent; clitellum developed over 1/3 XII-XVI (more so

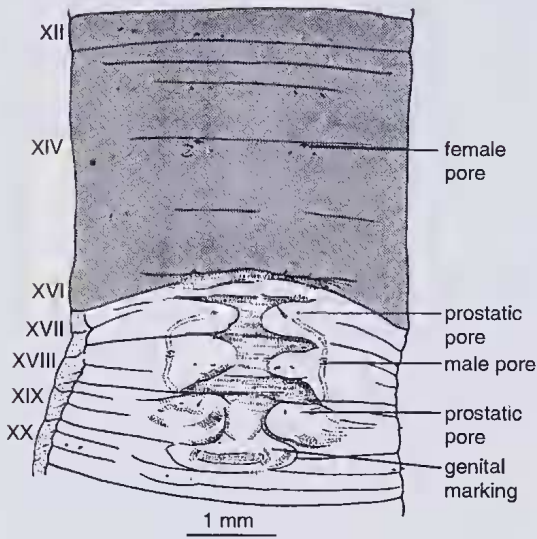


FIG. 2. *Diploptrema helonoma* sp. nov. Male genital field. Holotype (ANICGD.95.144.1).

dorsally, where it extends to beyond 1/2 XVII). ♂ pores 2 orifices at the midpoints of a pair of narrow, ill-defined (shallow) seminal grooves linking the prostatic porophores of a side; the ♂ pores are located barely presetally on XVIII, in *bc*, closer to *b*. Dependent on the state of muscular contraction during fixation, the ♂ field (defined laterally by the seminal grooves, anteriorly by a rhomboidal tumescence, and posteriorly by another marking), may be either generally concave, which sharpens the relief of the porophores, and the ridge joining the ♂ pores, or of fairly uniform contour. The former condition is presumably assumed during copulation, when the genital orifices would need to be raised for adpression to a partner. The porophores are coincident with the penial seta openings; the setae may be protruded in preserved specimens (H, P4), or withdrawn (P1, P3); in the former case, each porophore would appear to have only a single seta protruding at any one time. ♀ pores a pair of pre-setal slits, roughly aligned with *ab*, on XIV. Spermathecal pores 2 pairs in 7/8 and 8/9, each with a prominent presetal lip, and with posteriorly adjacent tumescences associated with the genial seta follicles. Accessory markings: a large, unpaired median rhomboidal (or elliptical) swelling in 16/17 (developed to a greater or less extent in all clitellate specimens examined); a similar marking in 19/20; the ♂ field (divisible into 4 depressed

areolae in contracted specimens) is also glandular, occasionally (P4), with pore-like impressions. Septa: 5/6 thickened, 6/7-9/10 moderately muscularised, remainder thin. Dorsal blood vessel single, continuous onto the pharynx; last hearts in XIII, the commissurals in X-XIII large, and latero-oesophageal; the supra-oesophageal vessel is traceable from VI to XIV, attaining maximal size in VI-IX, where its increased importance apparently corresponds to a decline in the size of the dorsal vessel. The remaining commissurals decrease in size anteriorly, and are dorso-ventral only. Gizzard small, soft and readily compressed, though with a slight muscular sheen, in V; oesophagus moderately wide, vascular, in VI-XVII, calciferous glands or conspicuous outpouchings absent. Intestinal origin in XVII, dilating gradually posteriorly, typhlosole lacking.

Holonephric: nephrostomes conspicuous on long necks in *ab*; avesiculate ducts open in line with *c*-setae, entering the parietes slightly anterior to the setal arc; nephridial bodies are enveloped in thin peritoneum, appearing as regular wafer-like units in each segment. Anterior tufting is absent.

Holandric: 2 pairs of brightly iridescent spermathecal funnels are present in X and XI, and 2 pairs of large, acinous seminal vesicles in IX and XII, the latter pair conspicuously the larger, and occupying virtually the entire ventral portion of that segment. Prostatic glands 2 pairs of coiled, tubular organs which encroach on posterior segments to a greater or lesser degree, penetrating the septa. The anterior pair is always the larger of the two. The prostatic ducts are short, straight and slightly muscular. The entire prostatic region is covered ventrally with a glandular mass that appears to be an internal manifestation of the ♂ field, and which may be responsible for secretions necessary for successful copulation. The prostatic ducts and penisetal follicles pass through this mass prior to discharging to the exterior. Penisetal follicles (consisting of conjoined *a* and *b* setal components) are equipped with little copulatory musculature; the setae are moderately long and gently arcing, the ectal 1/8 ornamented with irregularly spaced, rounded, deep scallops of variable diameter with somewhat jagged overhangs; these become more scattered and shallower entally. Length of mature setae = 1.9mm, midshaft diameter = 36.2µm (mean of 3).

Ovaries, consisting of flabelliform clusters of oocytes, and medium-sized ovarian funnels, present in XIII; no ovisacs demonstrable. Spermathecae 2 subequal pairs in VIII and IX,

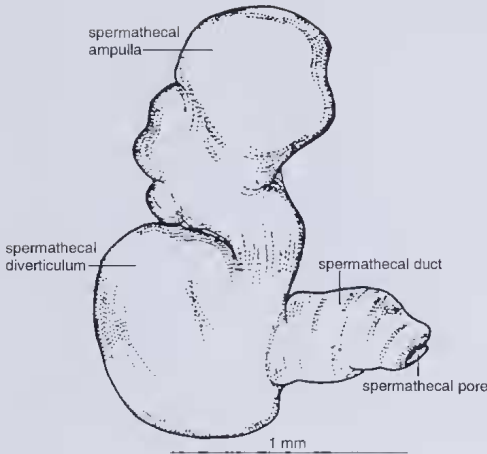


FIG. 3. *Diplotrema helonoma* sp. nov. Left spermathecal of segment IX. Paratype 1.

discharging anteriorly in their segments; each consisting of a bipartite ampulla: a clavate or irregular sacciform portion, connected by a broad neck to a subspherical component. A small, hemispherical 'diverticulum' is sessile on the latter, opposite to the point of attachment of the clavate section of the ampulla; a medium-sized duct is shared by the ampulla and diverticulum; the latter is brightly iridescent, containing numerous intramural sperm chambers. Length right spermatheca of IX = 1.7mm (base of ampulla to pore). Conspicuous genital seta follicles are associated with the spermathecae; these are surrounded by prominent, discrete, whitish glands, of which there is one per follicle in IX, and two in VIII. These glands are prostate-like, both in overall morphology and histologically, with a definite central lumen leading to small ducts discharging at the point of emergence of the genital seta from the body wall; their function is unknown. The setae are fairly straight, ornamented over the ectal portion of the shaft (including the somewhat swollen apical region) with conspicuous longitudinal fluting; this appearance is due to the alignment of long roughly parallel scallops with fairly smooth edges. Length of mature seta = 1.34mm; midshaft diameter = 35.1 $\mu$ m (mean of 3).

REMARKS. *Diplotrema helonoma* is the geographically closest species to *D. fragilis*. The similarities in overall morphology shared by the two taxa leaves little doubt as to their phylogenetic propinquity. Points of divergence include the much reduced gizzard in *D. helonoma*, differ-

ences in the position of the seminal vesicles and the dorsal pores and the conspicuous development of genital seta glands in *D. helonoma*.

***Diplotrema proserpinensis* sp. nov.**  
(Figs 4, 5)

ETYMOLOGY. Named for the type locality.

MATERIAL. HOLOTYPE: QMG5449. Myrtle Creek, between Cannonvale and Proserpine, (20°23'S, 148°36'E). CEQ; frequent in mud in the bottom of and in the bank of a stagnant backwater. Coll. B.G.M. Jamieson, 15 Jul 1966. PARATYPES 1-3: QMG2887, 2892, 2893, collection data as for holotype. OTHER MATERIAL: QMLGH2888, collection data as for holotype.

DESCRIPTION. Length = 103, 82mm. Width = 1.5mm. Segments = 225, 175 (H, P1). Form cylindrical, anterior end slightly bulbous over several segments, pale in alcohol. Prostomium pro-epilobous, dorsal pores absent. Setae closely paired throughout, ventral setal couples of XVIII present, those of XVII and XIX modified as enlarged penial setae, often protruding through the prostatic pores; those of VIII replaced by genital setae, situated on strongly protuberant papillae. Nephropores not externally recognisable.

Clitellum not developed.  $\delta$  pores seen slightly presetally, lateral of *b*-lines, in shallow seminal grooves that link the porophores of a side; prostatic pores 2 pairs, on medianly inclined dome-shaped papillae at the *ab* loci of XVII and XIX. The ventral body surface is depressed within the area circumscribed by the four prostatic papillae and extending as far as intersegment 16/17 and 19/20, its margins raised on each side as a longitudinal ridge along which the seminal grooves run.  $\text{♀}$  pores minute, presetal in *a* or *b* lines of XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, seen as elliptical areas, in *b*-lines.

Accessory markings: large, glandular pad, approximately circular in outline occupies most of XX between the *a* setae, and encroaches somewhat into XIX. This marking is developed only in the holotype to any significant degree, very faintly in P1, and not seen in any other specimens examined.

Septa: none strongly muscularised, but those anterior to and excluding 9/10 somewhat thickened. Dorsal blood vessel single, last hearts in XIII; of all the commissurals in VII-XIII, only those in XII and XIII are large and heart-like. Further vascular details not determinable owing to the small size of the species and pronounced bleaching. Gizzard large, in V; oesophagus narrow, moniliform, in VI-XIX, lacking pouching or

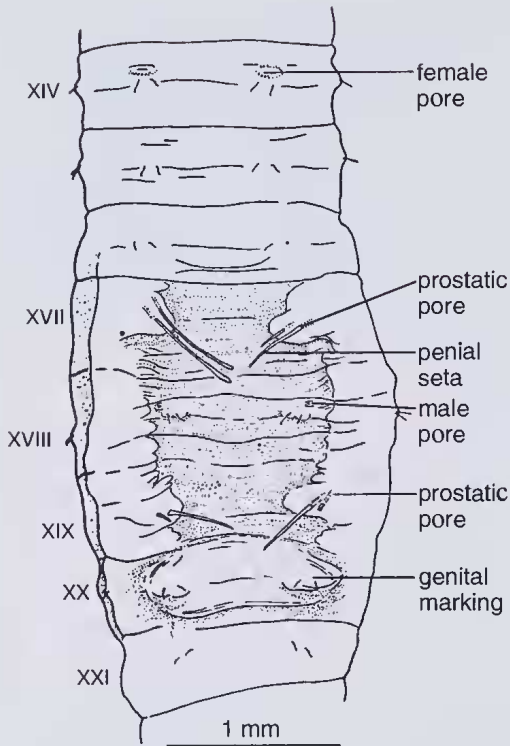


FIG. 4. *Diplotrema proserpinensis* sp. nov. Male genital field. Holotype (QMG5449).

calciferous glands. Intestine commences in XIX or XX, a well-developed oesophageal valve present at 18/19 or 19/20; typhlosole absent.

Nephridia present at least as far forward as VIII, stomate, their avesiculate ducts entering the parietes in a single series on each side, in *c*-lines; pharyngeal tufting absent.

Holandric: 2 pairs of very large, iridescent spermathecal funnels, and sperm masses, free in X and XI; seminal vesicles lobed, in XI and XII, those of XII filling the segment longitudinally, those of IX smaller. Prostatic glands slender tubes, those of XVII slightly tortuous, and extending into XIX or XX; those of XIX much smaller, tortuous, extending into XX; each with a slender duct. Penisetal follicles well-developed, each extending into its next posterior segment, four or more setae to a bundle. The setae curved gently, or through as much as a semicircle, ornamented over the distal sixth by a series of widely-separated, minute, distally directed teeth, some or all of which are members of transverse circlets; the distal extremity of the setae are 'laterally' widened, and terminally form a bulb with or without a small, apical point. Length

mature seta = 0.75mm, midshaft diameter = 27.3 $\mu$ m (mean of 2).

Ovaries, each with several strings of large oocytes, and funnels, present in XIII, ovisacs absent. Spermathecae two pairs, in VIII and IX, the posterior pair almost twice as large as the anterior. Each with a large, somewhat irregular ampulla, and a stout duct, at the ectal end of which, medially, is a single, large, ovoid diverticulum which may be almost as large as the ampulla. Length left spermatheca of IX = 0.66mm. Large genital seta follicles present in VIII, apparently associated with a glandular manifestation; the setae fairly straight, the ectal 1/3 ornamented with a series of longitudinal scallops, giving a serrated appearance. Length mature seta = 0.75mm (mean of 3), midshaft diameter = 27.3 $\mu$ m.

REMARKS. The absence of dorsal pores in this species may be connected with its semi-aquatic mode of existence, since this loss is also seen in the primarily limnic families Alluroididae, Biwadriidae, Almidae, Lutodrilidae, Sparganophilidae and the marine littoral megascolecid *Pontodrilus* (see Jamieson, 1988). It is presumably a response to the superfluity of coelomic fluid lubrication in aquatic habitats. *D. cornigravei*, which also lacks dorsal pores, is not necessarily related to members of the *D. fragilis* species-group. The disappearance of dorsal pores in the former species, recorded 'from swampy ground' (Jackson, 1931), has probably occurred convergently.

Whereas the gut contents of *D. helonoma* consist almost entirely of soft, partially digested organic matter, the upper alimentary tract of *D. proserpinensis* was found to contain, inter alia, numerous irregular quartz grains (especially in

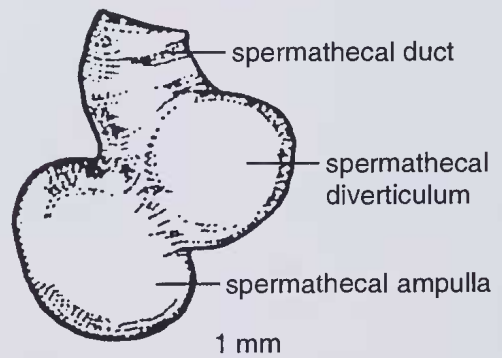


FIG. 5. *Diplotrema proserpinensis* sp. nov. Left spermatheca of segment IX. Holotype (QMG5449).

the gizzard). A dietary divergence may therefore account for the differential development of the gizzard in the two species.

## LITERATURE CITED

- BLAKEMORE, R.J. 1997. Two new genera and some new species of Australian earthworms (Acanthodrilidae, Megascolecidae: Oligochaeta). *Journal of Natural History* 31: 1785-1848.
- DYNE, G.R. 1978. A new species of *Microscolex* (*Diplotrema*) from New South Wales. *Proceedings of the Linnean Society of New South Wales* 103(1): 37-41.
1984. Systematics and zoogeography of Australian megascolecoid earthworms. Unpubl. PhD thesis University of Queensland, St Lucia.
- JACKSON, A. 1931. The Oligochaeta of Western Australia. *Journal of the Royal Society of Western Australia* 17: 71-136.
- JAMIESON, B.G.M. 1971. A review of the megascolecoid earthworm genera of Australia. Part II - The subfamilies Ocnodrilinae and Acanthodrilinae. *Proceedings of the Royal Society of Queensland* 82(8): 95-108.
1988. On the phylogeny and higher classification of the Oligochaeta. *Cladistics* 4: 367-410.
- JAMIESON, B.G.M. & BENNETT, J. 1979. New species of Acanthodrilinae and a new genus of Perionychini (Oligochaeta: Megascolecidae) from New Caledonia, their phylogeny and Zoogeography. *Bulletin de la Musée National de Paris 4e ser.*, 1, 1979(2): 353-403.
- JAMIESON, B.G.M. & DYNE, G.R. 1976. The acanthodriline earthworm genus *Microscolex* (*Diplotrema*) in the Northern Territory of Australia. *Australian Journal of Zoology* 24: 445-76.
- MICHAELSEN, W. 1907. Oligochaeten von Australien. *Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg*. XXX Band, 1 Heft.
1910. Oligochaten von verschiedenen Gebieten. *Mitteilungen aus dem Naturhistorischen Museum in Hamburg* 27, 2: 47-169.
1913. Die Oligochaten von Neu-Caledonien und den benachbarten Inselgruppen. Pp. 173-280. In Sarasin, F. & Roux, J. (eds) *Nova Caledonia, Zoologie*, vol. 1 L. III, No. 5. (C.W. Kreidals: Weisbaden).
1916. Results of Dr E. Mjöberg's Swedish scientific expedition to Australia 1910-1913. XIII Oligochaten. *Stockholm Kungliga Svenska Vetenskapsakademiens Handlingar* 52(13): 1-74.
1921. Zur Stammgeschichte und Systematik der Oligochaten, insbesondere der Lumbriculiden. *Archiv für Naturgeschichte* 86(1920), Abt. A.
- SPENCER, W.B. 1900. Further descriptions of Australian earthworms, Part I. *Proceedings of the Royal Society of Victoria* 13 (ns)(1): 29-67.
- STEPHENSON, J. 1930. *The Oligochaeta*. (Oxford University Press: Oxford).
- SWEET, G. 1900. On the structure of the spermiducal glands and associated parts in Australian earthworms. *Journal of the Linnean Society, Zoology* 28: 109-139.